

## THE IMPACTS OF GALLS AND GALLMAKERS ON PLANTS

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*Abstract.*—Gallmakers may have a number of negative impacts on host plants. In this paper, we report several negative effects of the tephritid *Eurosta solidaginis* (Fitch) on the composite *Solidago altissima* L. This gallmaker's impacts are appreciable on ramets (individual shoots) and include decreased leaf and inflorescence allocation, reduced rhizome numbers, redirection of host resources to the gall, and the loss of rhizome connections between galled ramets and the remainder of the clone. Because of localization of the gallmaker's impact and the clonal nature of the host plant, gallmaker impacts are negligible in mature clones. However, gallmaker attack on an establishing clone can reduce the lifetime fitness of its host. The results for this one gallmaker can not be generalized to other gallmakers, as the effects of each gallmaker will vary depending upon gallmaker seasonal cycles, host clonality, organs attacked, tissues stimulated, reactions, and the degree of resources mobilized. By detailing gallmaker impacts, we will gain insights into the selection pressures, evolutionary responses, and degree of reciprocal adaptation in plant-gallmaker interactions.

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Herbivory by gallmakers has the potential to result in a number of negative impacts on host plants. This paper is an attempt to detail some of those negative effects. However, because it is premature to make generalizations about the impacts of all gallmakers, we will detail one gallmaker's impact with the hope of stimulating additional studies.

Gallmakers, unique among herbivores, alter the development of plant tissues to form a tumor-like growth from which the gallmaker gains both nutrition and protection (Abrahamson and Weis, in press). It is likely, then, that the impacts of gallmakers are more severe than those of other herbivores when measured on a per herbivore basis. Further, it is important for us to view the gall phenotype as a result of the interactions between two genotypes: the gallmaker's, coding for the stimulus, and the plant's, for the reaction. It follows that the evolution of these two genotypes could be intimately tied to one another.

Gallmakers, as plant parasites, should evolve the means to manipulate their hosts so as to balance immediate gains with the future availability of suitable hosts. This could mean in some gallmaker-host systems that the gallmaker will evolve to minimize its impact on its host plant. Likewise, host plants, if sufficiently damaged by gallmakers (and other herbivores), should also evolve characteristics to reduce these impacts. This might include the elaboration of chemical defenses

or a reduction in reactivity to the gallmaker. These evolutionary possibilities suggest the importance of examining gallmaker impacts in light of unilateral versus reciprocal adaptation. Gallmaker-host plant interactions form one of the better systems to critically evaluate the "co-" in coevolution.

The negative impacts of gallmakers infesting certain agricultural crops are well documented (e.g. grape phylloxera, Hessian fly; Riley and Howard, 1891; McColloch, 1923). But, the frequency and degree to which gallmakers injure their hosts in natural situations is still open to question. Some workers have suggested that gallmaker impact is negligible (Wangberg, 1978; Gandar, 1979), however, quantitative analyses have repeatedly shown that galls are metabolic sinks for carbon (Fourcroy and Braun, 1967; Jankiewicz et al., 1970; Hartnett and Abrahamson, 1979; Weis and Kapelinski, 1984; McCrea et al., 1985), energy (Stinner and Abrahamson, 1979), and some mineral elements (Palct and Hassler, 1967; Abrahamson and McCrea, 1986). Obviously, when reproductive tissues are affected by gallmakers, the potential for negative impact is high (Harris, 1980; Collins et al., 1983). It is clear that as gallmakers procure their nutritional requirements they not only "rob" the host plant of the consumed tissue, but they also cause the plant to alter tissue that would otherwise serve productive functions in plant growth and reproduction (Abrahamson and Weis, in press).

Unfortunately, few gallmakers have been examined from the perspective of the impacts on their hosts. We do, however, have a growing body of data for one stem gallmaker, the tephritid *Eurosta solidaginis* (Fitch). This *Eurosta* attacks a hexaploid composite, *Solidago altissima* L. (tall goldenrod), and directs the formation of the goldenrod ball gall. Because this host is a rhizomatous, long-lived perennial, we must examine gallmaker impacts at two levels: the individual shoot (ramet) level and the genetic individual (genet) level. It is the latter level that is most crucial to understanding the potential for plant evolutionary responses to the gallmaker. In addition, we must use several currencies to measure these impacts since gallmakers use proteins for structural building blocks while their hosts use carbohydrates (Abrahamson and McCrea, 1986).

We have determined ball gallmaker impacts are appreciable at the ramet level in each of several currencies. An energy flow model, using ramet production, gall growth, and gallmaker growth, respiration, and egestion, showed that approximately 7% of the ramet's energy goes to support the ball gall and gallmaker (Stinner and Abrahamson, 1979). We have also found appreciable concentration of mineral elements (e.g., N and P) by two gallmakers that attack goldenrod. The ball gall and its gallmaker, for example, account for approximately 3.5% of a ramet's N (Abrahamson and McCrea, 1986). In another study examining biomass allocation as influenced by ball gallmakers, it was found that gallmakers decreased leaf and inflorescence allocation and reduced new rhizome numbers and biomass (Hartnett and Abrahamson, 1979). This latter finding is especially intriguing as it suggests the possibility of a carry-over of a gallmaker's impact into a subsequent season. To examine this, we induced galls in small two-ramet clones during the 1984 growing season. After overwintering, these clones were grown in the absence of gallmakers. Clones with 1 or 2 galls in 1984 had significantly fewer ramets in 1985 than the ungalled control clones (McCrea and Abrahamson, unpublished data). Thus, genets which lose resources to this gallmaker during their first year or two could potentially suffer fitness losses over their lifetime.

In an attempt to clarify the ball gallmaker's impact on biomass allocation and photoassimilate translocation, we used  $^{14}\text{C}$  labeled  $\text{CO}_2$  introduced to individual leaves above and below galls of different sizes. We learned that large galls intercepted a significant portion of the photoassimilate moving through the stem, but that the gall did not mobilize photoassimilates towards it (McCrea et al., 1985). In a similar experiment that used two-ramet clones, we found that while defoliation of the ramet opposite the labeled ramet induced translocation of photoassimilates to the defoliated ramet, ball gall presence did not. Thus, the gallmaker's impact was localized, possibly as a result of either the gallmaker acting as a "good" parasite and/or the host's reaction (McCrea and Abrahamson, unpublished data).

In another experiment, we created three ramet clones and induced zero to three galls/clone. These clones were allowed to grow to reproductive maturity and then harvested. The most significant finding was that ball galled ramets were over twice as likely to be physically isolated from their clone as ungalled ramets (McCrea and Abrahamson, 1985). It comes as no surprise then that we found no significant gallmaker effects on biomass allocation at the clone level in this study or in a field study examining entire clones (Bresticker and Abrahamson, unpublished data). We can conclude that the impacts of the goldenrod ball gallmakers are reduced through localization. However, because the impacts can come early in the development of a genet, ball gallmakers can reduce the number of ramets in the later years of a genet's life and hence can reduce lifetime fitness (McCrea and Abrahamson, 1985).

The detailed studies of the goldenrod ball gall suggest that even though this gallmaker has appreciable impacts at the ramet level, its impacts are negligible in mature clones. Unfortunately, we can not extend these results to other gallmakers. The impact of each species of gallmakers will vary depending upon host clonality, host organs attacked, tissues stimulated, host reactions, gallmaker seasonal cycles, and the degree of mobilization of host resources by the gallmaker. For example, a leaf gallmaker could stimulate an appreciably greater degree of mobilization, since a single leaf may not produce sufficient resources for the gallmaker. The ball gall, as a stem gall, is in an ideal location to simply intercept resources.

We can illustrate this variation in impacts with an example from another stem gallmaker, the tenthredinid *Euura lasiolepis*, which attacks the arroyo willow, *Salix lasiolepis* (Craig et al., in press). Willow tissues, like tissues of many other plants, become less susceptible to galling with aging. However, Craig and his coworkers have shown that heavy sawfly galling stunts or kills growth distal to the gall and stimulates sprouting of previously dormant buds. The resulting young branches keep the clone susceptible to further galling. Craig et al. (in press) have termed this "resource regulation," in that the gallmaker is maintaining or increasing the resources available to its future generations on the same host. Obviously, this sawfly stem gallmaker affects its host in a markedly different manner than the goldenrod ball gallmaker.

There is little question that gallmakers unilaterally adapt to their host, but the question of whether true reciprocal adaptation occurs is still open. The plant defenses that result in the variation observed in host susceptibility to gallmakers (McCrea and Abrahamson, unpublished data), could be the product of "diffuse" coevolution (*sensu* Futuyma, 1983) rather than true reciprocal coevolution.

If we hope to understand the ecological and evolutionary framework of host plant-gallmaker interactions, we must examine a number of these interactions from the host's perspective. By detailing gallmaker impacts, we will gain important insights into the selection pressures and the resulting evolutionary responses. Gallmaker-plant systems have the potential to yield crucial perspectives on the degree of reciprocal adaptation.

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